THE ARCHEGONIUM OF SPHAGNUM SUBSECUNDUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 199

GEORGE S. BRYAN

(WITH PLATES IV–VII)

This paper is planned as the first of a series on the life history of *Sphagnum subsecundum*, the work being undertaken through interest in the Sphagnales aroused during a course in the special morphology of Bryophytes under Dr. W. J. G. LAND at the University of Chicago. It is hoped that this investigation may not only bring to light new facts in the life history of *Sphagnum*, but when completed may enable us to determine more accurately the position of the Sphagnales in the phylogeny of the Bryophytes.

Field study

The first stage in this undertaking, that is, securing material for study, has been something of a problem in itself. The impression prevails, in some quarters at least, that *Sphagnum* seldom bears sex organs. For example, CAMPBELL (**1**, pp. 163–164) in a general discussion of the Musci says: "When the plants are dioecious it sometimes happens that the two sexes do not grow near together, in which case, although archegonia may be plentiful they fail to be fecundated and then no capsules are developed. This no doubt accounts for the extreme rarity of the sporogonium in many mosses, although in other cases, e.g., *Sphagnum*, it would appear that the formation of sex organs is a rare occurrence."

On the other hand, those investigators who have made studies of the sex organs of *Sphagnum* seen to have had little difficulty in securing material. LEITGEB (**8**) alone reports his study of the archegonium hampered by lack of material.

Again, there is disagreement as to whether or not the archegonial branches have characters by which they may be distinguished. As is well known, antheridial branches on approaching maturity are marked by their coloration. Have the archegonial branches such a well defined character? CAMPBELL (**1**, p. 177), referring

to the Sphagnales, says: "The archegonia are found at the apex of some of the short branches at the summit of the plant, which externally are indistinguishable from the sterile branches." CAVERS (**2**, p. 295), on the contrary, says: "The female branch grows for some time in the same way as an ordinary sterile branch, but the leaves visible from the outside of the branch become rapidly longer in passing from below upward, so that the branch takes the form of a loose, tapering, pointed bud, deep green in color, and stands out sharply from the vegetative branches associated with it."

Furthermore, there is some disagreement as to the time of the appearance of sex organs. According to SCHIMPER (**10**), antheridia are produced at any time, but are most abundant in autumn and winter. WALDNER (**11**) found mature antheridia and archegonia under the snow in February. GAYET (**3**) reports having spent much time searching for archegonia in the winter, but only in the spring did he find them developing. However, he emphasizes the point that he does not wish to say archegonia are not produced at all in the winter, but rather that it is only in the early spring time one finds them being formed in the greatest abundance.

To summarize, we find: (1) sex organs are believed by some to be of rare occurrence; (2) there is disagreement as to the recognition of archegonial branches; (3) there is some uncertainty concerning the time of the production of sex organs.

To investigate these points in regard to *S. subsecundum* we have made a careful study of a bog covering about 20 acres near Mineral Springs, Indiana, 40 miles south of Chicago. This place was selected for several reasons. It contains enough water in the spring to escape being burned over, the annual fate of many bogs in the vicinity of Chicago, hence the study could be carried on without fear of having the material injured by fire. Also in previous years some sporophytes had been noted here. Furthermore, polsters of a *Sphagnum* (later identified by Mr. E. J. HILL as *S. subsecundum*) were well scattered through the bog, affording a wealth of material.

Active work was begun the first week in November 1912. It soon became evident that *S. subsecundum* here studied is dioecious, and that when the sex organs are approaching maturity both

male and female plants have well marked characters. The antheridial heads are decidedly globose and show variations in color from yellow brown to red brown, occasionally almost black. The archegonial heads are less globose, have a somewhat flattened aspect on top, and show no unusual coloring except the conspicuous bud at the growing point in the center of the head. This bud varies in color from yellow brown to red brown. An analysis of the bud reveals archegonia almost mature on short side branches near the apex of the main axis, the coloring matter being in the perichaetial leaves surrounding the organs.

A careful study of the whole bog and others for several miles about disclosed the fact that not a single sterile head of *S. subsecundum* could be found. Sex organs were everywhere in vast numbers. In order to determine whether or not such a condition might be unusual, and to provide abundant material for study, developments through winter, spring, summer, and autumn of 1913 were closely followed; and again in the autumn of 1913 the sex organs appeared in the same vast numbers.

As far as *S. subsecundum* in the vicinity of Mineral Springs is concerned, we conclude therefore (1) that sex organs are not of rare occurrence; (2) that both antheridial and archegonial heads on approaching maturity are distinctly characterized by coloration; (3) that antheridia and archegonia begin to develop in August and September respectively, the antheridia always appearing first.

A brief statement of time relations in the developmental process of the archegonium as observed in the autumn of 1913 may be of interest. Young stages were first noted on September 16 and continued to appear for approximately four weeks. By October 25 the youngest archegonia were beginning the formation of canal cells, while the oldest were almost mature. At this time the coloring of the perichaetial leaves began to be noticeable. By November 15 the canal row had broken down in some of the oldest archegonia. Those archegonia which have not reached maturity on the advent of cold weather develop slowly through the winter. In the spring, therefore, at the time of the disappearance of the snow, it is possible to find stages having 7 or 8 canal cells, with the ventral cell not yet divided.

Methods

For this investigation almost daily killings were made, from the middle of September to the middle of November. The killing agent used was 0.25 chrom-acetic, cold, and heated to various temperatures up to 52° C., the best results obtained being at about 30° C. At this temperature there was practically no plasmolysis in the delicate young stages, and the quick penetration made certain the securing of any figures that might be present in the material. The higher temperatures were not satisfactory, causing more or less plasmolysis and leaving the material difficult to stain. Safranin in combination with Licht Grün, and Haidenhain's iron alum hematoxylin were used as stains.

Development of the archegonium

HISTORICAL

The archegonium of *Sphagnum* has been the subject of a number of investigations. Of the early papers the most important is the elaborate monograph of SCHIMPER (10). According to this investigator the archegonium, arising directly from the apical cell of a branch, begins its development by an apical cell with two cutting faces, just as in the true mosses, and forms in this manner about 6 cells. The events that follow, being beyond the technique of that time, are described in a hazy manner and may be passed over here. Paraphyses are said to occur among the archegonia.

The brief account given by HOFMEISTER (5) does not differ from that of SCHIMPER.

In 1869 LEITGEB (8), while working out the development of the antheridium, found a few female branches, and on each, one archegonium was being formed, arising directly from the apical cell of the branch, but whether the divergence of the division walls is one-half, as HOFMEISTER and SCHIMPER thought, or whether, as in the antheridium, there are smaller divergences, and furthermore from what cells the secondary archegonia arise, he is unable to say because of a lack of material.

The account given by JANCZEWSKI (7) in 1872 may be summarized as follows. The apical cell elongates and is divided by

cross-walls, finally consisting of 3 or 4 cylindrical cells, each of which makes secondary divisions, and above these two cells whose walls are obliquely placed and which also make secondary divisions. The origin of the archegonium proper and the formation of adventitious segments and canal initials are declared to be the same as among the mosses. In *Sphagnum rigidum* and *S. acutifolium* "anomalies" in the development are reported, though the regular process described above also occurs. No explanation is offered as to what these "anomalies" are. It is to be regretted that no illustrations accompany the article.

The most recent account is that given by GAYET (3) in 1897. He agrees with LEITGEB that the first archegonium is axillary, but dismisses the early stages with the brief statement that "the first divisions are normal." The two figures given to illustrate this are by no means clear, so that one is left in doubt as to the meaning of the word normal. GAYET is unable to find the two cells with oblique walls reported by JANCZEWSKI and thinks them an error of interpretation. The neck of the archegonium is said to elongate by the division of the terminal cell, and this terminal growth is produced without giving rise to canal cells.

From these brief reviews it is evident that there is little agreement among investigators as to developmental processes, and that the whole subject is in a haze of uncertainty.

EARLY STAGES IN THE DEVELOPMENT OF THE ARCHEGONIUM

In the autumn, at the time of the production of sex organs, the elongation of the main axis is checked, so that the newly formed branches whose apical cells are being transformed into archegonia appear as a cluster or bud about the main axis at the apex. This transformation of the apical cells of the side branches into archegonia is not simultaneous, but proceeds acropetally, occurring earlier and earlier in the development of each branch as one passes toward the apex. As yet this transformation process has not been observed to reach the apical cell of the main stem, though more than 400 slides bearing on this point have been examined.

In the material studied the maximum number of archegonia arising from an apical cell is three. In such a case each of the

two segments last formed becomes the initial of a secondary archegonium, while that portion of the apical cell above and not included by them is the initial of the primary archegonium (fig. 2). Fig. 3 shows this in cross-section. A few examples have been noted where one of the secondary segments, after making several divisions, has for some reason been checked and remains as a slight projection on the base of the mature primary archegonium. In some cases only the last formed segment develops as a secondary archegonium; while still more rarely no secondary archegonia are formed at all, the apical cell becoming the initial of a single archegonium (fig. 5).

THE PRIMARY ARCHEGONIUM

The primary archegonium shows a remarkable variation in the manner of its early divisions. The first wall may be transverse (fig. 6) or slanting (fig. 4). If the first wall is slanting, the second may be transverse (fig. 5). However, by the examination of a large number of slides one may recognize two general types of development. A filament of cells, usually 4 or 5 in number, may be formed by successive transverse divisions of the apical cell (figs. 6–9). Four or five cells may be produced by the activity of an apical cell with two cutting faces (figs. 11, 12); this is probably the most frequent method. Between these two extremes there may be various mixtures of planes. An interesting intermediate condition in which the walls do not quite intersect is shown in figs. 10 and 13.

At this point the question may be asked, Why are not figs. 6–9 merely the development of an apical cell with two cutting faces seen at an angle of 90° from the plane represented by figs. 11 and 12? This matter has been carefully examined and the following facts presented as an answer. Unquestionably the walls may have such an appearance, but the test is their behavior under the oil immersion lens. If the walls are transverse, they remain steady on focusing up and down; but if of the kind formed by an apical cell with two cutting faces, they swing in a characteristic manner as one changes the focus. Frequent examples of this have been found, as well as those in which there was no shifting.

Hence figs. 6–9, belonging to this latter class, are known to be transverse.

THE SECONDARY ARCHEGONIUM

The secondary archegonium shows a greater degree of uniformity. The initial divides into an inner and an outer cell (figs. 6, 10). This outer cell by subsequent transverse divisions (figs. 8, 9, 14) gives rise to a filament of cells, 5 or 6 in number, in each of which the usual secondary divisions occur (fig. 16*b*). As yet no evidence has been found that the secondary archegonium may develop by an apical cell with two cutting faces.

THE DEVELOPMENT OF THE ARCHEGONIUM PROPER

After there has been formed, as described above, a filament of cells by transverse walls, or a series of cells by an apical cell with two cutting faces, and secondary divisions have occurred in each segment except the terminal one, the development of the archegonium proper begins in the manner usual among the Bryophytes. In the terminal cell, which becomes somewhat enlarged, three oblique walls appear, cutting off three peripheral segments and originating a large cell within, which has the form of an inverted truncated pyramid (figs. 13, 14). This large cell we shall designate the primary axial cell. On division it gives rise to an outer axial cell, the cover cell, and an inner axial cell, the central cell (figs. 17–19). The wall cells of the archegonium arise from the three peripheral segments.

Up to this point the development of the archegonium proper coincides exactly with the description given by numerous investigators for the archegonium of the Bryophytes, whether Hepaticae or Musci. It is in the events immediately following that there is a divergence of views and theories. For the sake of continuity we shall postpone the presentation of these theories until later and continue the description of the developmental processes.

Here then the important question arises, What is the part played by the cover cell and what by the central cell in the further development of the archegonium? The answer must be found in a study of sections both longitudinal and transverse.

THE COVER CELL

Figs. 18 and 19 represent typical cases in the appearance of the archegonium with cover cell and central cell formed. It will be noted that the two cover cells differ in size. This is due to the peculiar shape of the cover cell, coupled with the direction of the cut. In fig. 18 the cut is median through the long diameter; in fig. 19 through a shorter diameter. This may be more clearly understood by an examination of the cover cells as shown in transverse sections (figs. 53–55).

It is important to note that the cover cell may divide by a vertical wall into two almost equal segments before the division of the central cell takes place (figs. 21, 54). But more important still is the evidence that by the time the central cell has completed its division into primary neck canal cell and primary ventral cell, the cover cell has at least become divided by a vertical wall into two almost equal segments (figs. 22, 24), and in some cases has formed a quadrant of cells (figs. 23, 56). The division lines between the cells of the cover and the outer cells of the neck are clearly marked and easy to follow in the younger stages. Thus in figs. 29–32 the cover is literally the cap of the archegonium, and in each case contains 6 cells (three each in median longitudinal section, as illustrated). In fig. 33 the cover consists of 8 cells. However, in the older stages the cells of the cover and the neck usually merge so insensibly that the two cannot be separated with any degree of certainty. Hence no accurate statement as to the final number of cells produced by the cover can be made.

From the foregoing facts it is evident that the cover cell divides early by a vertical wall into two almost equal segments. Subsequent vertical divisions in each of these segments produce a plate of cells, 8 or more in number, which covers the apex of the archegonium and in mature forms merges insensibly with the upper cells of the neck. There is not the slightest evidence to show that the cover cell cuts off any basal segments.

THE CENTRAL CELL

The division of the central cell into primary neck canal cell and primary ventral cell is shown in figs. 20 and 21. The primary

neck canal cell is the mother cell of the neck canal row. The spindle for the division into two canal cells, as shown in fig. 25, has been found four times in the material studied. From this point on the cells of the canal row divide in almost any order. The evidence for this shown by the spindles in figs. 27, 28, 30, 31, and 34. By this intercalary growth a row of canal cells, usually 8 or 9 in number, is formed (figs. 38, 40).

The division of the primary ventral cell occurs late. Fig. 38 shows 8 canal cells and the ventral cell undivided; while we were fortunate enough to find a spindle when there were 7 canal cells (fig. 39). The ventral canal nucleus produced by this division is peculiar, being only a trifle smaller than the egg, and is remarkable in that it is regularly persistent and behaves for a time just as does the egg. Not long after the division into ventral canal cell and egg, the canal row begins to disintegrate (this process having a variable beginning, through quite often acropetal), but not so the ventral canal cell. Its cytoplasm begins to condense about the nucleus (the same process occurring about the egg), and soon we have in a mature archegonium the appearance of two eggs separated by a wall (fig. 41). Later the cytoplasm about each of these two nuclei becomes markedly condensed and rounded off and may be easily observed in the living material. Still later the wall between the two cells breaks down and the nuclei, each as the center of a ball of cytoplasm, come to lie near together in the venter of the archegonium. Usually just before fertilization the ventral canal nucleus disintegrates.

THE GROWTH OF THE ARCHEGONIUM

We have already shown that the growth of the canal row is intercalary. The same is true of the growth of the wall cells. Fig. 26 gives valuable evidence on this point. It is not an exceptional case, but was found a number of times. The evidence goes to show that about the stage of two canal cells there comes a sudden vigorous growth of the archegonium through intercalary divisions, this process frequently involving one or two rows of cells simultaneously. This sometimes results in one side of the archegonium becoming longer than the other, tilting the cover, as is shown in

figs. 33–35. In the older stages the growth is slower, but spindles in various cells of the periphery give further undoubted evidence of intercalary growth.

THE MATURE ARCHEGONIUM

In the account of the development of the archegonium given by the various authors already mentioned there has been much discussion concerning the mature archegonium. It will be of interest, therefore, to record the facts in regard to *S. subsecundum*. The archegonia here may be divided into two classes or types, those long and slender and those massive. This difference begins to appear early and may be clearly seen by a comparison of figs. 30 and 32 or 34 and 35. Naturally, therefore, we find variability in the mature stages. In its simplest portion, the neck for a short distance may have 6 rows of cells, or in the more massive types each cell of the 6 rows may have one or more secondary divisions. Fig. 58 represents a typical series through the simplest portion of such a neck. The neck merges gradually into the venter, which is usually 4 cells thick (fig. 59), though simpler venters may also be found.

ABNORMALITIES

Abnormalities are of rather frequent occurrence in *S. subsecundum*. Double venters (fig. 42), unequal division of the venter, the ventral canal nucleus larger than the egg (fig. 43), ventral canal nucleus the same size as the egg (fig. 44), and multiple eggs (fig. 45) are not of rare occurrence.

THE ABSENCE OF PARAPHYSES

SCHIMPER (**10**) in his elaborate monograph reports structures among both antheridia and archegonia which he calls paraphyses. Other investigators have been unable to find any trace of paraphyses. We have taken particular pains to investigate this in *S. subsecundum*, dissecting hundreds of heads, both antheridial and archegonial, but not the slightest indications of paraphyses could be found. This was further confirmed by an examination of about 500 slides with the same result. In a few cases the branched hyphae of a fungus, *Tilletia Sphagni*, were observed

about some of the archegonia. This, as has already been suggested by several investigators, may account for the so-called paraphyses of SCHIMPER. We feel safe, therefore, in stating that so far as *S. subsecundum* is concerned there are no paraphyses about either the antheridia or the archegonia.

THE MUCILAGE HAIRS

The peculiar structures developing in the axil of each young leaf have been commented on by several investigators. A complete series in the development may be easily followed out. One of the axillary cells at the base of the leaf becomes papillate (fig. 47), divides into an upper cell and a basal cell (fig. 49), and the upper cell makes two acropetal divisions resulting in a filament of three cells (figs. 49, 50). This is the mature stage. The terminal cell of the filament usually becomes enlarged and is filled with a dark staining substance, probably mucilage. Several mucilage hairs may arise from the axillary row at the base of a leaf (fig. 49). Occasionally branched forms may be found (fig. 51). As the leaf grows older the hairs disappear.

Discussion

So far as the young stages in the development on the archegonium are concerned, it appears that HOFMEISTER (5), SCHIMPER (10), and JANCZEWSKI (7) are all correct. An examination of many sections shows development by all the methods reported, as well as intermediate conditions not reported. In the development of the archegonium proper we are unable to find any evidence to support the statement of JANCZEWSKI (7) that adventitious segments and canal initials are cut off as in the Musci. Furthermore, the evidence is clear and emphatic that the growth of the archegonium is not terminal, as GAYET (3) holds, but is intercalary. The spindles shown in various figures are conclusive on this point.

We must now consider briefly the theories of archegonial development among the Bryophytes, and the natural question as to what bearing this investigation has upon these theories.

JANCZEWSKI (7), GOEBEL (4), CAMPBELL (1), HOLFERTY (6), and others hold that the archegonium of the Musci is to be distin-

guished from that of the Hepaticae by its peculiar apical growth; that in the Musci the canal cells do not arise by the activity of one mother cell as in the Hepaticae, but are produced in part by the division of the cover cell. This cover cell cuts off two sets of segments, the one being parallel to the axis of the archegonium and forming the wall cells of the neck; the other parallel to the base of the archegonium and contributing to the neck canal row.

The view presented by GAYET (3) is in the main a contradiction. He holds that in both Hepaticae and Musci the growth of the archegonium is terminal, but no internal segments are added to the canal row by the cover cell, which cuts off segments forming the wall cells of the neck.

SERVETTAZ (9, pp. 169–171) in a recent paper has advanced a new interpretation of archegonial formation. His description of the development in *Phascum cuspidatum* may be summarized as follows. The initial cell divides transversely and gives a basal cell and a superior cell. The superior cell then divides obliquely a certain number of times, from two to five; then one of the cells placed below the terminal cell divides tangentially and determines the formation of a central cell, which by basipetal divisions gives a row of 8 cells, the canal row, the ventral canal cell, and the egg. The evidence offered for these statements certainly is not convincing, and if true this origin of the central cell differentiates *Phascum* from any of the Bryophytes now known.

The evidence we have presented for *Sphagnum* has nothing in it to support the views of SERVETTAZ (9) and GAYET (3). Furthermore, it breaks the distinction between Musci and Hepaticae drawn by JANCZEWSKI (7), CAMPBELL (1), GOEBEL (4), etc. Here at least is one of the Musci in which the cover cell does not add to the canal row.

Conclusions

The archegonium of *Sphagnum subsecundum* is synthetic. The stalk, the thick venter, and the comparatively slender twisted neck are moss characters; the relatively inactive cover cell, the intercalary growth of the archegonium, and the low number of canal cells are hepatic characters as we know them today.

Summary

1. During the autumns of 1912 and 1913 sex organs have been found in vast numbers on *Sphagnum subsecundum* in the vicinity of Mineral Springs, Indiana.

2. On approaching maturity the archegonial heads may be recognized by the colored bud in the center of the head at the apex. Analysis of the bud shows terminal archegonia on short side branches.

3. The archegonia begin to develop in September.

4. The apical cell of a side branch is a primordium; each of the two segments last formed becomes the initial of a secondary archegonium, while that part of the apical cell above and not included by these segments is the initial of the primary archegonium.

5. There is great irregularity in the early stages of the development of the primary archegonium: there may be a filament of cells by the successive transverse divisions of the apical cell; or growth by an apical cell with two cutting faces; or a mixture of planes.

6. As yet the secondary archegonium has been found to develop only by the successive transverse divisions of the apical cell.

7. The archegonium proper is initiated in the manner usual among the Bryophytes. In the terminal cells three oblique walls cut off three peripheral segments and originate the primary axial cell within, which on division gives rise to cover cell and central cell.

8. The cover cell is relatively inactive and cuts off no basal segments.

9. The central cell on division forms the primary neck canal cell (the mother cell of the neck canal row) and the primary ventral cell.

10. The growth of the neck canal row is intercalary, the cells dividing in almost any order.

11. The primary ventral cell divides late into ventral canal cell and egg.

12. The growth of the wall cells of the archegonium is intercalary.

13. The mature archegonium has 8 or 9 canal cells.

14. The breaking down of the canal row may begin at any point, is frequently acropetal, but never involves the ventral canal cell.

15. The ventral canal cell is persistent, behaves for a time exactly as does the egg, but normally disintegrates just before the archegonium opens for fertilization.

16. Abnormalities, such as double venters, multiple eggs, etc., are of common occurrence.

17. The archegonium of *Sphagnum* is synthetic, combining certain characters of the Hepaticae with others of the Musci.

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UNIVERSITY OF CHICAGO

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EXPLANATION OF PLATES IV–VII

All figures were drawn with aid of Abbé camera lucida at table level, and, being reduced one-half in reproduction, now show the following magnifications: figs. 1–35, 43–56, ×525; figs. 36–42, 57, ×300; figs. 58–59, ×180.

Abbreviations are as follows: *a*, primary archegonium or its initial; *b*, *c*, secondary archegonia or their initials; *l*, leaf.

PLATE IV

FIG. 1.—Primordium showing a primary initial and one secondary initial.

FIG. 2.—Tangential section through primordium, showing primary initial and two secondary.

FIG. 3.—Same in transverse section; dotted line shows plane of cut in fig. 2.

FIG. 4.—First wall in primary initial slanting; secondary initial has divided to form an inner and an outer cell.

FIG. 5.—First wall in archegonium initial slanting, second transverse; no secondary formed.

FIG. 6.—First wall of primary initial transverse.

FIG. 7.—Uppermost wall of primary initial transverse; next below tilts slightly; secondary not shown.

FIG. 8.—Two transverse walls in primary archegonium; secondary shows first transverse wall.

FIG. 9.—Three uppermost stories of primary archegonium formed by transverse walls.

FIG. 10.—Walls of primary archegonium do not quite intersect.

FIG. 11.—Development of the primary archegonium by an apical cell with two cutting faces; first transverse wall has appeared in the secondary archegonium.

FIG. 12.—The same, slightly older.

FIG. 13.—Stalk of archegonium formed chiefly by walls that do not intersect; in terminal story the primary axial cell has been originated by the three oblique walls.

FIG. 14.—Stalk of primary archegonium regular; primary axial cell cut out; median longitudinal section through secondary archegonium showing two transverse walls.

FIG. 15.—Tangential section through secondary archegonium showing two transverse walls.

FIG. 16.—Group consisting of primary archegonium and two secondary; the primary and one secondary shown in outline.

FIG. 17.—Division of primary axial cell into cover cell and central cell.

FIG. 18.—Cover cell and central cell.

FIG. 19.—The same.

FIG. 20.—Division of central cell into primary neck canal cell and primary ventral cell.

FIG. 21.—The same, but shows cover cell divided.

FIG. 22.—Primary neck canal cell and primary ventral cell formed; cover cell has divided into two almost equal segments; plastids beginning to be conspicuous about each nucleus.

FIG. 23.—The same, but cover is forming a quadrant; the cell on the left shows a figure, while that on the right has divided in the same plane.

PLATE V

FIG. 24.—Primary neck canal cell and primary ventral cell; unequal growth in the walls pushing cover to one side.

FIG. 25.—Primary neck canal cell in division.

FIG. 26.—Two neck canal cells and the primary ventral cell; intercalary growth in the walls of the archegonium, pushing cover to one side; plastids becoming conspicuous.

FIG. 27.—Slender type of archegonium with two neck canal cells and the primary ventral cell; the uppermost neck canal cell is in division.

FIG. 28.—Simultaneous division of the two neck canal cells.

FIG. 29.—Three neck canal cells and primary ventral cell; cover has 6 cells (three shown in median longitudinal section).

FIG. 30.—Slender type of archegonium with three neck canal cells and primary ventral cell; figure in terminal neck canal cell; cover as above.

FIG. 31.—Three neck canal cells and primary ventral cell with figure in basal neck canal cell; cover as above.

FIG. 32.—Massive type of archegonium; four neck canal cells and primary ventral cell; cover as above.

FIG. 33.—Five neck canal cells and primary ventral cell; cover, tilted to one side, has 8 cells (4 shown).

FIG. 34.—Five neck canal cells and primary ventral cell; the middle neck canal cell is in division.

FIG. 35.—Six canal cells and primary ventral cell; cover, irregular through disturbance, has 8 cells; plastids conspicuous in the canal row.

FIG. 36.—Symmetrical type of archegonium, having 6 neck canal cells and primary ventral cell; cover difficult to follow, but probably has 8 cells (4 shown).

FIG. 37.—Seven neck canal cells and primary ventral cell.

PLATE VI

FIG. 38.—Eight neck canal cells and primary ventral cell.

FIG. 39.—Seven neck canal cells and primary ventral cell in division to form ventral canal cell and egg.

FIG. 40.—Nine neck canal cells, ventral canal cell, and egg.

FIG. 41.—Neck canal cells broken down; protoplasm beginning to round off about ventral canal nucleus and egg.

FIG. 42.—Fine example of double venter.

FIG. 43.—Unequal division; ventral canal nucleus larger than egg.

FIG. 44.—Elongated venter almost equally divided; ventral canal nucleus same size as egg.

FIG. 45.—Venter with 4 cells; the 3 lowest probably are eggs, the uppermost the ventral canal cell.

FIG. 46.—Median longitudinal section through cap of mature archegonium, showing unusual divisions.

FIG. 47.—Section tangential to face of leaf; first stage in the development of mucilage hair; axillary cell at base of leaf becomes papillate.

FIG. 48.—Nucleus has divided and papillate cell cut off by a wall.

FIG. 49.—Acropetal division of the papillate cell.

FIG. 50.—Second acropetal division of the papillate cell; the mature mucilage hair.

FIG. 51.—Branched form of mucilage hair.

PLATE VII

FIG. 52.—Series of transverse sections through young primary archegonium and two secondary.

FIG. 53.—Serial sections through archegonium proper, showing cover cell and central cell.

FIG. 54.—Serial sections; the cover cell has divided, but central cell is yet undivided.

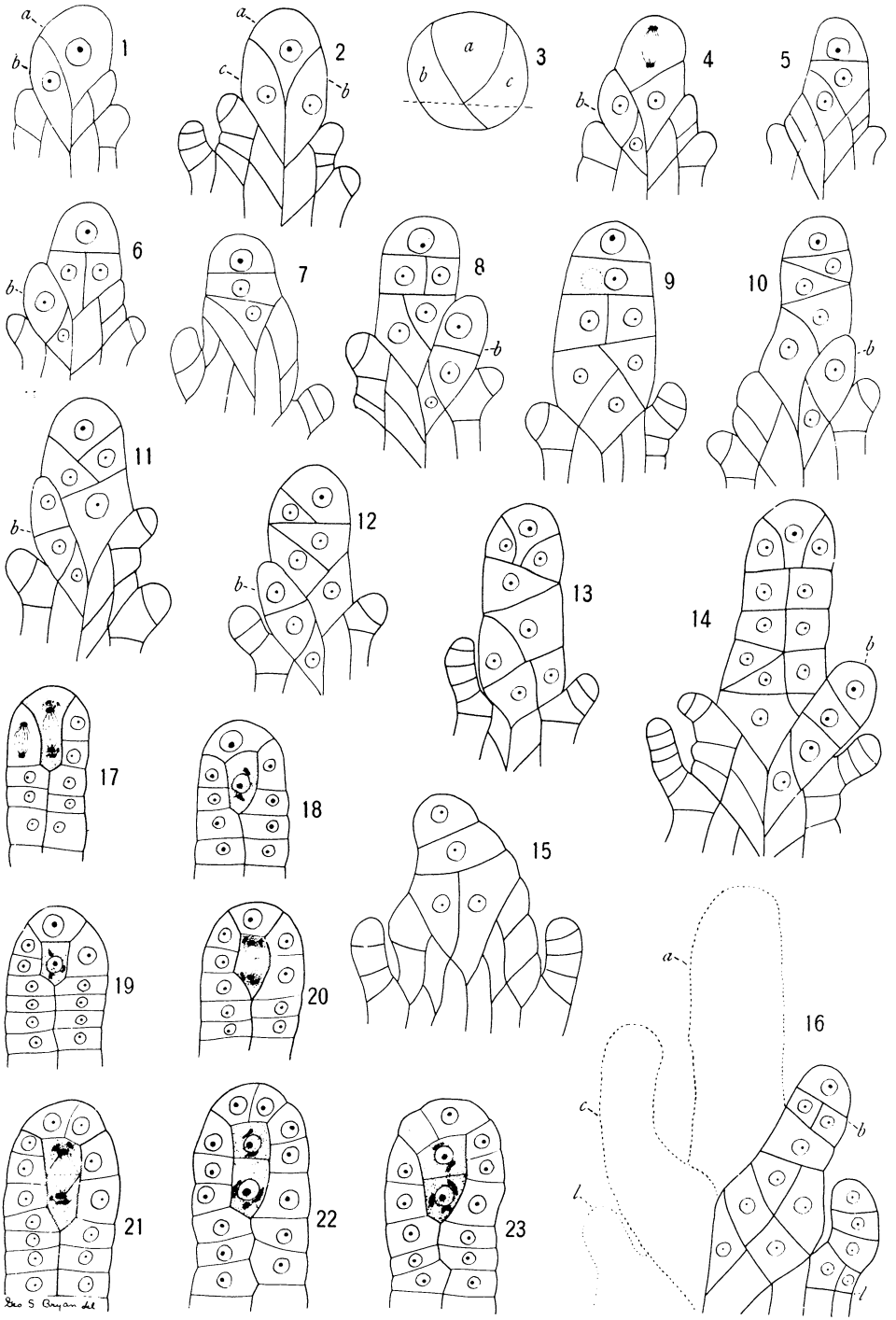
FIG. 55.—Serial sections, showing in the formation of the archegonium proper the three oblique walls which have cut off the peripheral segments and originated the primary axial cell within.

FIG. 56.—Serial sections through archegonium having primary neck canal cell and primary ventral cell; the cover cell has formed a quadrant of cells.

FIG. 57.—Serial sections through archegonium with 6 canal cells and ventral cell; the cover contains 8 cells; the gradual transition from cap to neck to venter is well shown.

FIG. 58.—Serial sections through simplest portion of neck of mature massive type of archegonium; section *A* shows the characteristic thickenings toward the cap.

FIG. 59.—Venter of same series at level of egg nucleus.



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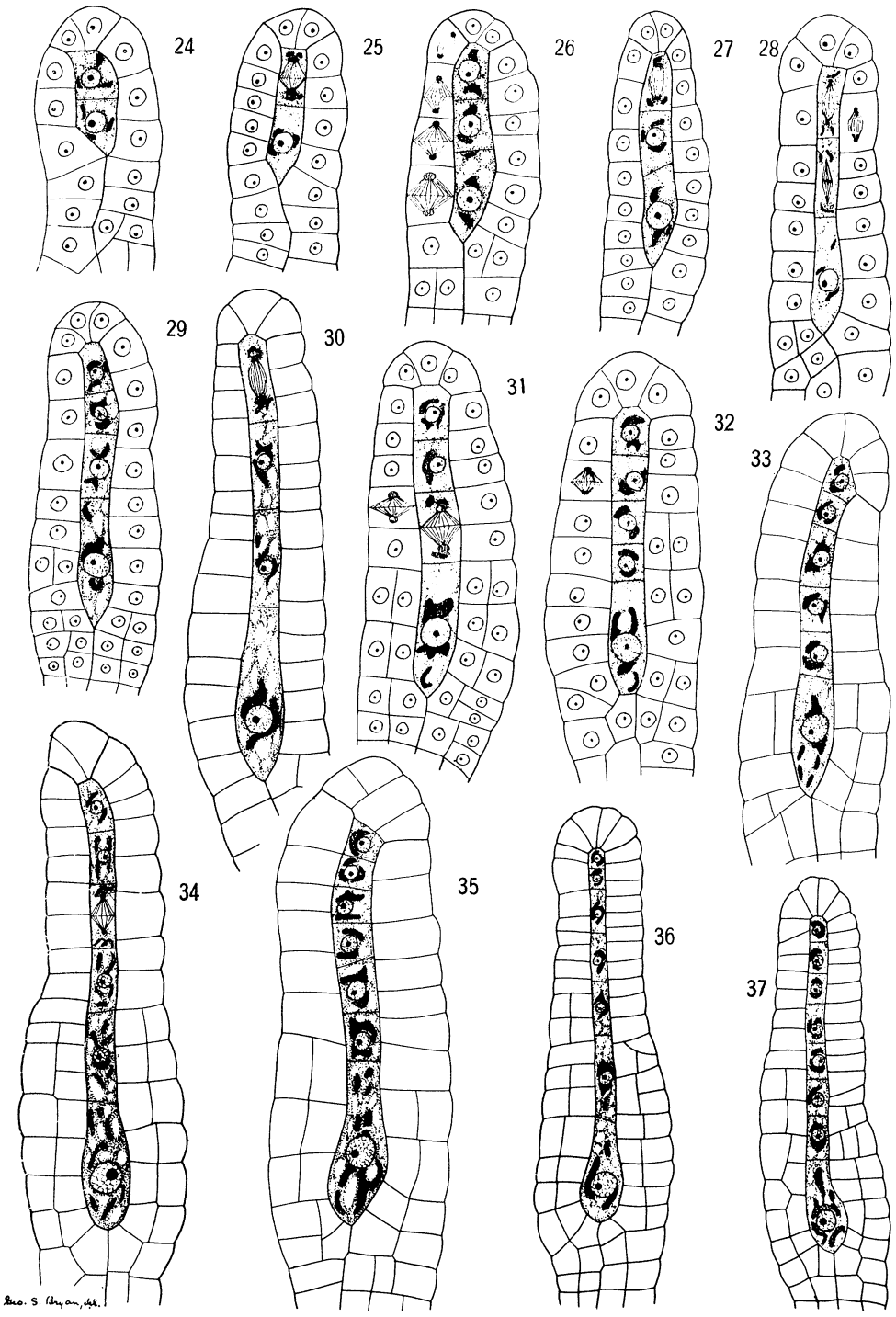

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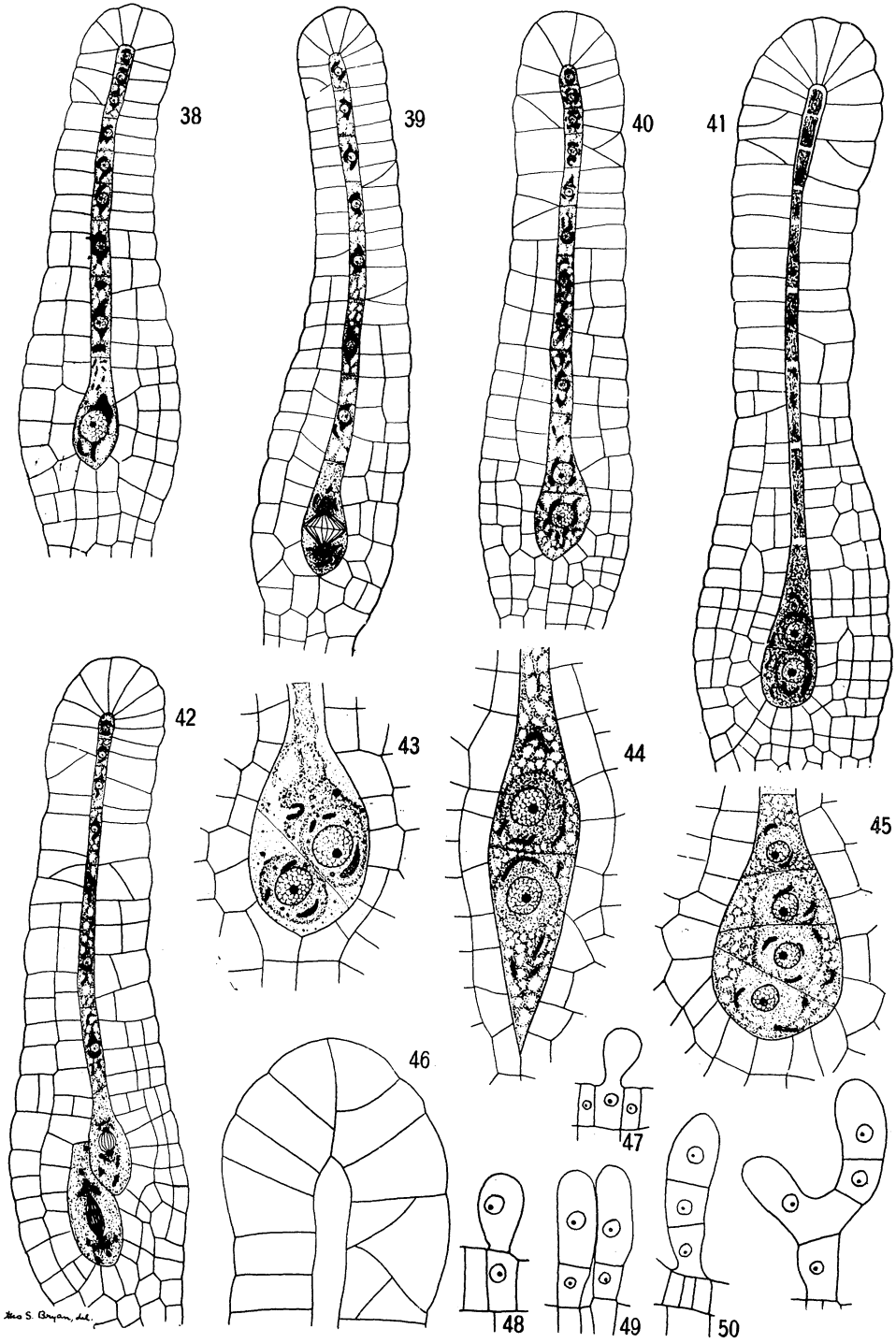

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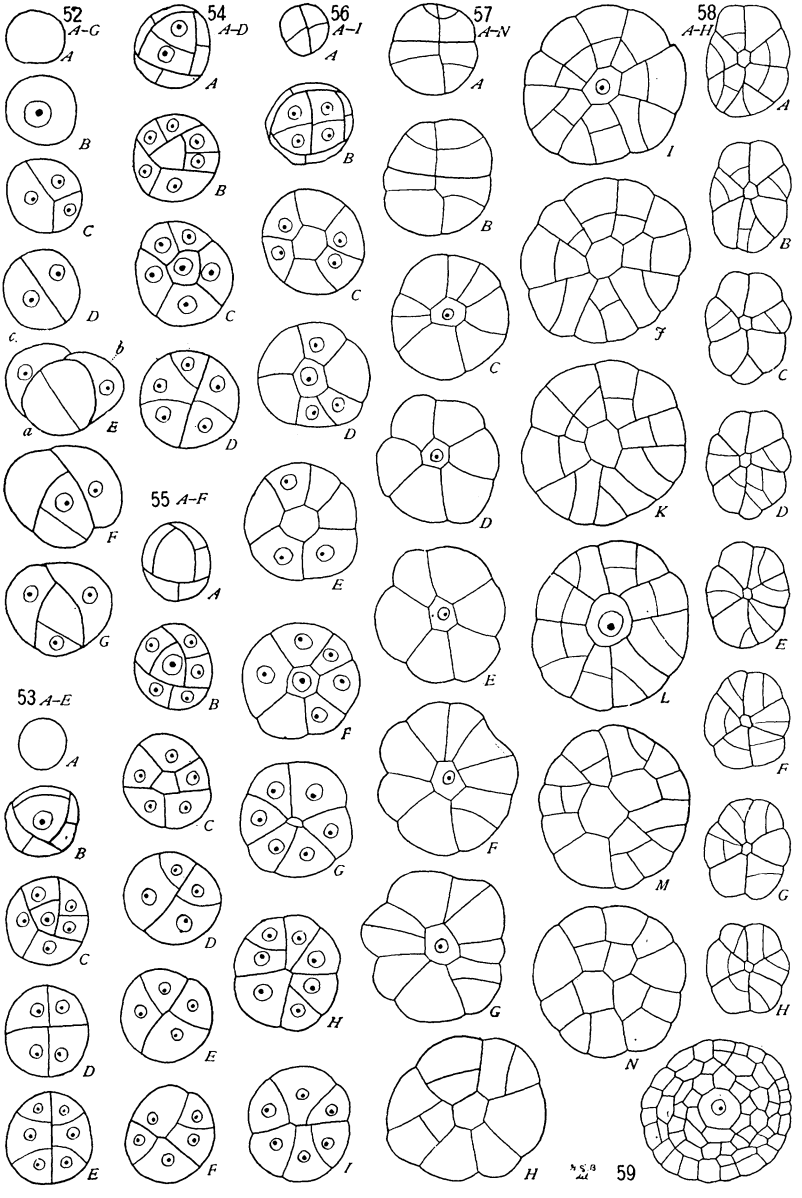

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